REDESCRIPTION OF *NEPHRURUS ASPER* GÜNTHER, AND DESCRIPTION OF *N. AMYAE* SP. NOV. AND *N. SHEAI* SP. NOV.

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Three allopatric species, clearly defined by morphology and colour pattern, comprise the *N. asper* species complex. *N. asper* is confined to Queensland (10°53'S-25°21'S), and has a distinctive, boldly banded colour morph occurring on Cape York Peninsula (extending south to Mt Surprise, 18°21'S); *N. amyae* sp. nov. to the south-central Northern Territory and *N. sheai* sp. nov. to the Kimberley region of Western Australia and the Arnhem Escarpment of the Northern Territory. All three species occur in open woodland habitats where they feed on a wide range of arthropod species. Males are in reproductive condition during the summer months and gravid females are present in the population from mid-summer to autumn for *N. asper* and *N. amyae*. *N. sheai* may be sexually active throughout the year. □ *Gekkonidae, Nephrurus, systematics, new species, distribution, open woodland, diet, reproduction.*

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Nephrurus asper was described from a single specimen (BMNH1946.8.23.34) from Peak Downs Stn, mideastern Queensland (22°56'S, 148°05'E). Subsequently, specimens matching the type description have been recorded from most of northern Australia (Cogger, 1992).

While the distinctive morphology of *N. asper* has ensured its nomenclatural stability (Cogger et. al., 1983), several authors have commented on geographical variation within the species. Storr (1963) noted differences in tail length between specimens from Western Australia and Queensland. Bauer (1990) observed that specimens from the south-central Northern Territory were larger than those in other parts of the range. Wilson and Knowles (1988) recognised the broad-banded form of *N. asper* from Cape York Peninsula as distinct from other populations of this species.

An examination of all *N. asper* held in the collections of major Australian museums revealed that the species, as currently recognised, could be divided into four geographically distinct groups (Arnhem Escarpment, NT & Kimberley region, WA; south-central NT; Queensland & Cape York Peninsula) on the basis of colour, pattern, spinosity, and other scale characters. Pattern and spinosity have been used widely in gekkonid revisionary work (Couper et. al., 1993; Storr, 1988, 1989). They have been found to be useful in delineating the species in the *N. asper* complex, in a way which conforms closely with statistical analyses.

The current study is augmented by Kolmogorov Smirnov Two-sample Tests and multivariate discriminant analyses. These analyses, performed using body measurements and quantitative scale counts only, provide an independent assessment of the morphological identity of the four geographic groups identified on colour pattern and/or degree of spinosity.

The statistical analyses were conducted by one of us (RAMG) and the taxonomic analysis was conducted by the other (PJC)

All measurements were taken using Mitutoyo electronic callipers. Abbreviations for body measurements are as follows: snout-vent length (SVL); axilla to groin (AG); tail, tip to constriction at base (T); tail, tip to vent (TV); knob width (KW); forelimb, axilla to tip of longest digit (L1); hindlimb, groin to tip of longest digit (L2); neck length, axilla to posterior edge of ear (NL); head length, tip of snout to dorsal/anterior margin of ear (HL); head width, measured between ear openings (HW); head depth, from above eyes to ventral margin of maxillae (HD); snout, tip to anterior margin of orbit (S); eye to ear, posterior margin of orbit to anterior margin of ear (EE). Abbreviations for scale counts and caudal annuli are as follows: number of granular scales in direct contact with dorsal edge of rostral scale (R); number of interorbital scales counted across the narrow, bony bridge between the orbits, includes the enlarged series of scales on either side (I); number of supralabial scales counted to exclude granular scales towards angle of mouth (SL);

TABLE 1. Differentiation between groups using a KS2 Procedure χ^2 from the 6 possible comparisons between the 4 samples. N is the number of contrasts with KS2d χ^2 statistic >6. The .05 level for χ^2 is about 5.99, for the .01 level is about 9.21, for the .001 level is about 13.81.

	GROUPS					
body character	1 vs 2	1 vs 3	1 vs 4	2 vs 3	2 vs 4	3 vs 4
T	6.59	3.69	4.94	4.00	0.47	3.88
TV	18.00	5.81	3.24	5.83	0.52	2.31
KW	6.50	7.53	0.24	22.99	3.88	1.61
TA	9.44	4.30	4.10	0.35	0.59	0.44
L1	1.35	4.34	1.80	1.05	0.92	0.44
L2	0.52	3.98	1.81	2.07	0.48	2.57
HW	0.70	8.03	1.33	7.16	0.41	5.63
HL	0.26	7.19	0.59	4.88	1.11	1.44
S	1.31	7.11	2.14	9.20	3.71	5.87
NL	6.32	6.17	1.58	15.64	1.44	3.07
SL	25.32	24.93	17.59	1.24	2.55	3.44
IL	35.80	26.48	15.38	0.73	2.41	1.32
R	3.40	30.75	0.79	30.13	3.79	9.45
I	19.84	35 28	6.04	7.42	0.20	2.84
EE	2.97	0.92	7.50	4.19	2.85	7.32
HD	0.09	5.43	1.98	4.60	2.10	7.78
AG	0.32	2.35	1.65	1.37	1.11	0.26
N	8	9	4	6	-	3

number of infralabial scales counted to exclude granular scales towards angle of mouth (IL), and number of caudal annuli counted between basal constriction and distal knob (TA).

OTHER ABBREVIATIONS USED: Queensland Museum (QM), Australian Museum (AM), Museum of Victoria (NMV), South Australian Museum (SAM), Western Australian Museum (WAM) and the Northern Territory Museum (NTM), Cape York Peninsula (CYP), mideastern Queensland (MEQ), Queensland (QLD), Northern Territory (NT), Western Australia (WA).

Reproductive and dietary data were compiled by examination of specimens in which the body cavity had already been opened.

STATISTICAL ANALYSES

The following data analyses have been performed, using complete records on 149 animals. Some are internal checks on consistency and are hence not reported in full here. The characters used in these analyses are the body measurements and scale counts defined above. Group 1 = the Arnhem Escarpment (NT) & Kimberley region (WA), group 2 = QLD, group 3 = south-central NT, and group 4 = CYP.

1. The Kolmogorov Smirnov Two-sample Test (KS2) (Kolmogorov, 1941; Smirnov, 1939) on each of the 6 pairwise contrasts between groups on each of 17 characteristics, giving a total of 10 χ^2 values each with 2 d.f. This is a nonparametric procedure, using minimal prior assumptions about the form of frequency distributions of measurable characteristics (Walsh, 1965).

It indicates which characteristics differentiate better than al some given probability level, if the characteristics are independent. This is not strictly true a priori, and hence conservative probability levels may be used in deciding what results to accept. It also will fail to detect second-order measures, such as ratios or differences of characteristics, which can be non-linear and of use, unless these are built into the data. The measures in mm have been divided by SVL, those based on scale counts have not. Bilateral measures have been pooled (Table 1). Discriminant analyses have also been run because they can utilise linear (but only linear) combinations of characteristics, and hence may separate groups which are not distinguished on single characteristics (Table 1). The discriminant analyses do, however, make some distributional assumptions approximating to normality and homoscedascity across groups.

The role of the KS2 is also involved with the question of what characteristics to use in the discriminant analysis, if not all the characteristics which have been measured are used.

2. The correlation matrix on the characteristics over the whole 149 complete records used. This showed that the rank of the data is much less than 17; this indicated, as expected, that there is redundancy in the morphological data.

3. Four discriminant function analyses (Rao, 1952):

3.1. Using all the characteristics, on raw measures.

3.2. Using a stepwise discriminant analysis, on raw measures.

3.3. Using all the characteristics, on measures divided by SVL.

3.4. Using a stepwise discriminant analysis, on measures divided by SVL.

The stepwise procedures are inbuilt to the SPSSx program used; because of the intercorrelations noted under part (2) above, the variables retained in a stepwise analysis will depend on those intercorrelations and on the relative sizes of the four groups, but will be analogous to the

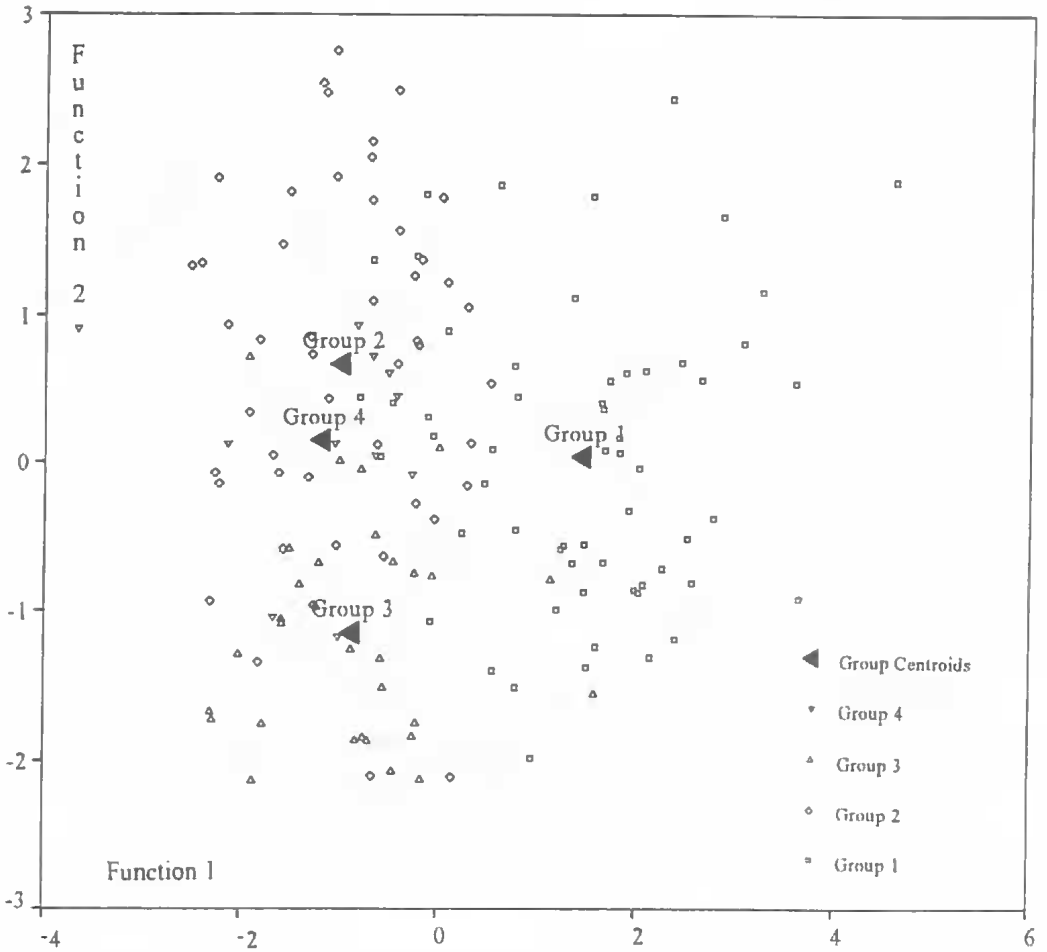

FIG. 1.Plot of the individuals and group centroids on the 1st two canonical variates from the discriminant analysis. Group 1 = the Arnhem Escarpment (NT) & Kimberley region (WA), group 2 = QLD, group 3 = south-central NT, and group 4 = CYP.

characteristics with larger χ^2 values in Table 1. We present tables derived from (3.4) here; as there are only 11 animals in the smallest group, the number of variables in the discriminant analysis has to be reduced to below 10. The stepwise procedure is the most appropriate for this, retaining only those variables with discriminative power; it showed by F-tests that only eight variables were legitimately retained in the analysis.

Information for the identification of new specimens when allocation is based on body measurements and scale counts only is not in itself sufficient (Tables 2, 3). Allocation to species must also take into consideration colour pattern and degree of spinosity. The relative values of the coefficients (Table 3) are of use, they are weights to multiply with corresponding measurements, and then sum the products and add the constant term in the column. As additional specimens become available it is preferable to incorporate them in a extended discriminant analysis, thus yielding new weights. The efficiency of allocation decisions using this discriminant analysis is summarised (Table 4); it will be noted that the relatively poor separation of group 2 (QLD) and group 4 (CYP) is compatible with the results from the KS2 analysis.

RESULTS

The plot of individuals and group centroids on the first two canonical variates from the discriminant analyses (Fig. 1) gives a picture com-

TABLE 2. Standardised discriminant function coefficients and correlations with discriminant functions from the stepwise analysis with three canonical functions. Ic = coefficients for the first discriminant, Ir = its correlations with discriminating variables, and so on.

char	Ic	Ir	IIc	IIr	IIIc	IIIr
HW	.070	.112	.511	.475	-.706	-.415
I	1.453	.388	-.209	.470	-1.234	-.201
LI	.392	.187	-.459	.102	-.472	.107
NL	-.161	-.118	.398	.432	-.207	.191
R	-.114	.204	1.147	.737	1.023	.159
SL	.864	.360	-.367	.358	1.121	.122
TA	-1.750	.081	.122	.431	-.956	-.086
TV	-.577	-.327	-.138	.271	.124	-.122

patible with Tables one and four. Group 2 (QLD) and group 4 (CYP) are not significantly separable on external morphology. The recognition of group 4 was based on colour-pattern. The uniformity in morphology between groups 2 and 4 dovetails well with preliminary genetic data which show a low level of divergence between a broad-banded specimen from Heathlands, CYP and a specimen from the Capella region of MEQ (Couper & Donnellan, unpubl. data). All QLD material examined in this study, with the exception of the broad-banded specimens from CYP, is consistent with the holotype of *N. asper* (BMNH1946.8.23.34) in both colour-pattern and scalation (see Remarks for *N. asper*) and is here assigned to this taxon. The broad-banded CYP specimens are regarded as a geographically distinct colour morph of *N. asper*. The statistical analyses show that group 1 (Arnhem Escarpment, NT & Kimberley region, WA) and group 3 (south-central NT) are morphologically distinguishable from QLD and CYP combined as a single group (Table 1, Fig. 1) and also from each other. Groups 1 and 3 are here described as new, allopatric taxa. The recognition of these taxa is further supported by preliminary genetic data (Couper & Donnellan, unpubl. data).

The 'Atlas of Australian Resources' (Anon, 1952-69) shows reasonable conformity between the distribution of the *N. asper* species complex and the occurrence of upland country and heavy, often stony soils. However, the zoogeographical implications of this distribution can not be assessed without first establishing a phylogeny for the genus and determining the dates of speciation events. Presently, there is no fossil record for *Nephrurus* and biochemical studies are incomplete.

SYSTEMATICS

Nephrurus asper Günther, 1986
(Fig. 2A,B; Statistical analyses groups 2, 4)

MATERIAL EXAMINED

QUEENSLAND: QMJ22179, QMJ24921, Bamaga, Cape York Peninsula (10°53'S 142°24'E); QMJ57652, 6.5km E of Heathlands airstrip (11°44.33'S 142°38.28'E); QMJ54644, Heathlands road, 1km from main Cape road junction (11°46'S 142°40'E); QMJ40165, Weipa to Aurukun, mid-way, N Camp Beagle Airstrip (13°05'S 141°57'E); QMJ738, Kingsborough (16°55'S 145°02'E); QMJ4960, Bullock Ck, via Cairns (16°55'S 145°46'E); QMJ57993, QMJ58850, Elizabeth Ck, nr Bulleringa NP, N of Mt Surprise (18°00'21"S 145°59'50"E); QMJ2125, ? Northern Rivers; QMJ44689, New Moon Stn (19°12'S 145°44'E); QMJ3443, Charters Towers, Black Jack (20°08'S, 146°13'E); QMJ42015, Hughenden, approx 2km W of Iona-Redcliffe Stn Homestead (20°59'S 144°33'E); QMJ44948, Egera Stn (20°59'S 146°05'E); J143, Natal Downs (21°05'S, 146°09'E); QMJ4525-6, Kuridala, S of Cloncurry (21°17'S 140°30'E); QMJ15565, 80km SW of Mackay (21°39'S 148°42'E); QMJ31976, QMJ35040, Winton (22°23'S 143°02'E); QMJ5727, Lucknow Stn, W of Winton (22°43'S 140°55'E); QMJ1355, QMJ3552, Clermont (22°50'S 147°38'E); QMJ28699, Cork Stn via Winton (22°56'S 142°18'E); QMJ46720, Aramac Range, Winhaven Stn (22°57'S 145°41'E); QMJ56088, Capella, 20km N on Clermont road (22°59'S 147°53'E); QMJ36795, Moonggoo (23°10'S 148°04'E); QMJ3767, Rockhampton, Dalma, Waroula (23°20'S 150°32'E); QMJ9912, Longreach (23°26'S 144°15'E); QMJ7983, Mary Vale Stn, Yalleroi via Blackall (23°35'S 146°58'E); QMJ36794, E of Comet Stn (23°37'S 148°40'E), QMJ34205-06, half way up the Blackdown Tableland escarpment (23°37'S 14910'E); QMJ8080, Bogantungan (23°39', 147°18'); QMJ741, Diamantina Lakes (23°46'S 141°08'E); QMJ31545, Winton fossil site (23°50'S 142°15'E); QMJ9132, Blackall (24°26'S 145°28'E); QMJ43356-7, Moura, 4km S of junction of Theodore & Gibihi Roads (24°38'S 149°59'E); QMJ7878, QMJ10526, Jundah (24°50'S 143°04'E); QMJ4540, Dawson Valley, Castle Ck (24°50'S 150°20'E); QMJ6011, Weathersfield?; QMJ742, No locality data; AMR128183, Batavia Downs, Wenlock R (12°40'S 142°40'E); AMR128796, Cairns (16°55'S 145°46'E); AMR31773, Mt Fox nr Ingham (18°19'S 145°51'E); AMR113852, approx. 14.5km W of 'Mt Cooper', nr St Paul's vine scrub (20°31'S 146°55'E); AMR14183, 210km S of Charters Towers (21°38'S 146°55'E); AMR63065, approx. 48km NW of Clermont (22°25'S 147°23'E); AMR107703 N of Clermont (22°50'S 147°38'E); AMR120094, Mayne Junction Hotel, approx. 40km N of Diamantina Lakes Stn (23°33'S 141°22'E); AMR15107, Yamala (23°35'S 148°22'E); AMR113116, Diamantina Lakes Stn, SW of Winton (23°41'S 141°11'E); AMR55786, Duaringa (23°43'S 149°40'E); AMR110544, AMR110562,

camp, 14km NE of Scott's Tank, Diamantina Lakes, NW of Windorah (23°45'S 141°40'E); AMR130721-2, AMR130726, 20km W of Moura on Bauhinia Downs road (24°37'S 149°47'E); NMVDT-D182 (Donald Thomson Collection), Lower Archer R (13°30'S 142°00'E); NMVD7527, Mt Cook, Cooktown (15°28'S 145°15'E); NMVD2040, Queensland; SAMR14023, 22km NW of Cooktown (15°25'S 145°04'E); SAMR12594, Cooktown (15°28'S 145°15'E); SAMR15791, Charters Towers (20°05'S 146°16'E); SAMR1771, Mt Coolon (21°23'S 147°20'E); SAMR42600, 6km N of Diamantina Stn (23°43'S 141°08'E); SAMR42601-02, 4km N of Diamantina Stn (23°44'S 141°08'E); SAMR42603, 85km W of Windorah (25°21'S 141°50'E); WAMR55475-7, 16km W of Charters Towers (20°08'S 146°07'E); WAMR55552, WAMR55601-2, Fermoy Homestead, 88km S of Winton (23°10'S 143°02'E); NTMR1144, Clermont (22°50'S 147°38'E); NTMR266, Rockhampton (23°22'S 150°32'E).

DIAGNOSIS

N. asper is medium-sized and moderately spinose. It is distinguished from *N. sheai* by the colour pattern of its digits (digits unbanded vs digits strongly marked with alternating bands of brown and white); from *N. sheai* and *N. amyae* by its smaller size (max SVL 114mm vs 121mm *N. sheai*, 135mm *N. amyae*). It is further distinguished from *N. amyae* by the spinosity of the its rump and thighs (moderately spinose vs extremely spinose). The arrangement of the basal scales surrounding the tubercules on the rump and thighs also separates *N. asper* and *N. amyae*. In *N. asper* the basal scales are uniform in size and less than half the height of the central scale. In *N. amyae* the basal scales are irregular in size and in most specimens examined, some of the basal scales are greater than half the height of the central scale.

In the KS2 analysis *N. asper* (excluding broad-banded CYP specimens which are not significantly separable from other QLD populations of this species) and *N. amyae* show significant separation of the shape of frequency distributions for; KW, HW, S, NL, R, & I. *N. asper* (excluding broad-banded CYP specimens) and *N. sheai* show significant separation of the shape of frequency distributions for; T, TV, KW, TA, NL, SL, IL & I (Table 1).

DESCRIPTION

SVL(mm): 47-114 (N 74, mean 84.1). Proportions,(%SVL): - L1 - 36.8-47.8 (N 74, mean 43.0), L2 - 43.2-55.6 (N 73, mean 49.0), AG - 34.4-54.2 (N 74, mean 44.4), T - 11.4-22.2 (N 66, mean 16.4), TV - 15.7-27.4 (N 66, mean 22.7), HL - 27.9-34.8 (N 73, mean 31.3), HW - 23.9-30.6 (N 74, mean 27.7), HD - 10.7-15.8 (N 70, mean 13.8), S - 9.2-12.7 (N 74, mean 11.1), EE - 10.0-15.0 (N 73, mean 12.3), NL - 10.4-21.1 (N 72, mean 15.5).

TABLE 3. Fisher linear discriminant function coefficients. Animals are assignable to the species with the highest function, given their measurements corrected for SVL.

	GROUPS			
char	1	2	3	4
HW	841.13	841.40	785.09	881.74
I	-26.45	-134.19	-116.54	-95.68
L1	372.24	330.65	361.47	314.64
NL	36.29	67.61	33.14	47.55
R	-37.54	-12.84	-56.61	-50.85
SL	89.71	52.31	64.69	27.21
TA	-135.06	-18.37	-28.78	23.92
TV	-3.45	47.62	54.14	48.57
Const	-197.58	-193.83	-184.77	-195.18

Head. Large and deep, covered with small, round to hexagonal, juxtaposed scales. Posteriorly bearing scattered tubercules intermixed with the smaller scales. Each tubercule consists of a high central scale, circled by a ring of smaller basal scales. Tubercules most prominent on the nape. Dorsal skin co-ossified with skull. Nostril small, opening upwards and backwards. Eye large with vertical pupil. Ear vertically elongate, tympanum deeply recessed. Rostral scale small, with 8-17 (N 77, mean 12.5) scales in direct contact with dorsal edge. Interorbital scales 7-12 (N 76, mean 8.9). Supralabial scales 11-17 (N 152, mean 13.5). Infralabial scales 10-17 (N 152, mean 13.5).

Neck. Broad, less than half width of head.

Body. Stout, dorsal and ventral surfaces with small granular scalation. Granular scales intermixed with larger conical tubercules on dorsal and lateral surfaces. Mid-dorsal tubercules small,

TABLE 4. Classification results for 149 animals. Actual group by predicted group membership.

Actual Group	No. of Cases	Predicted Group Membership			
		1	2	3	4
Group 1	59	45	8	4	2
Group 2	48	2	30	7	9
Group 3	31	2	2	25	2
Group 4	11	0	2	1	8

rump tubercules moderate. Basal scales surrounding rump tubercules uniform and less than half as high as the central scale. Rump tubercules larger than flank tubercules (45% material examined) or subequal to flank tubercules (55% material examined). Rump tubercules smaller than nape tubercules (51% material examined)or subequal to nape tubercules (49% material examined). Lower flanks and ventral surface with scattered, slightly raised rosettes which vary between being pronounced or barely discernible.

Limbs. Long and slender, bearing enlarged tubercules on dorsal surfaces. Tubercules on thighs largest, with uniform basal scales less than half as high as the central scale. Digits short, cylindrical, undilated distally and terminating in a non-retractile claw. Third toe on hindlimb longest.

Tail. Short, moderately depressed, constricted at base and terminating in a globular, kidney-shaped knob (KW 17.8-38.8%T, N 66, mean 29.1). Usually four, rarely five or six longitudinal rows of tubercules present on dorsal and lateral surfaces. Uniform basal scales surrounding caudal tubercules less than half as high as the central scale. Caudal annuli 9-12 (N68, mean 10.4).

PATTERN

Body. In spirit, mid-dark brown, or mid-dark grey on dorsal surface. Many specimens have a broad black band on the nape. Seven - eight, rarely six, narrow irregular crossbands (crossbands broad and continuous in CYP specimens) present between head and hindlimbs. Crossbands range from obscure to bold and are continuous or broken into a series of spots, with each spot covering a tubercule. Fine black lines form reticulations which become obscure in larger specimens and can be difficult to see in darker individuals. Ventral surface cream, sometimes faintly marbled with grey or brown.

Limbs. Lacking irregular crossbands distally. Digits unbanded or only obscurely banded.

Tail. As for body, with an obscure, broad, pale crossband on proximal half.

Head. Sometimes slightly lighter than body. Covered dorsally and laterally with fine black reticulations, which form an intricate pattern. These reticulations are most prominent in juveniles and may fade in larger specimens.

DISTRIBUTION

From the drier parts of coastal MEQ through central and western districts. Also present on CYP (Fig. 3).

The locality given for QMJ2125 is '?Northern Rivers', which usually refers to an area in northern NSW. The following entry in the register (QMJ2126) is a specimen of *Saltuarius cornutus* from the same locality. Neither of these species occur in NSW, nor are they sympatric elsewhere. *N. asper* typically occurs in dry open country while *S. cornutus* is confined to rainforest habitats. Either the locality '?Northern Rivers' should be regarded as an error or it refers to a region (unknown to the authors) of southern Cape York Peninsula where both rainforest and dry forests occur.

HABITAT

N. asper favours rocky substrates in open woodlands (Steve Wilson, Tim Hawkes, pers. comm.). It has been recorded also from stony or compacting soil plains, where sheltering sites are available (Ehmann 1992; Couper, unpubl. data); from low heath at Heathlands, CYP, and Darwin Stringybark open forest, at Aurukun (Cameron & Cogger, 1992).

REPRODUCTIVE NOTES

Clutch size - two eggs. Egg-laying occurs in mid-late summer. Female WAMR55476 was gravid during late February. The two oviducal eggs measured 27.1 X 13.8mm and 25.2 X 14.0mm; QMJ54644 had a greatly enlarged vitellogenic follicle in each ovary at the time it was killed in early February, 1992. The largest of these measured 9.67 X 7.28mm. A gravid female was brought to Wild World for identification in mid-April (T. Hawkes, pers. comm.). Male WAMR55552 was in reproductive condition (epididymis enlarged and turgid) in late November.

DIETARY NOTES

The gut of QMJ56088 contained two cricket legs (Orthoptera: Gryllidae). QMJ36795 contained a medium-sized centipede (Chilopoda: Scolopendridae) and an ant. QMJ44689 contained fragments of a medium-sized spider, and a medium-sized cockroach (Blattodea: Blattidae). Two faecal samples were collected at Heathlands, CYP, in late January 1992. The first sample contained a large spider, a small centipede, a large coleopteran larva and small to medium-sized cockroaches (Blattodea). The second sample

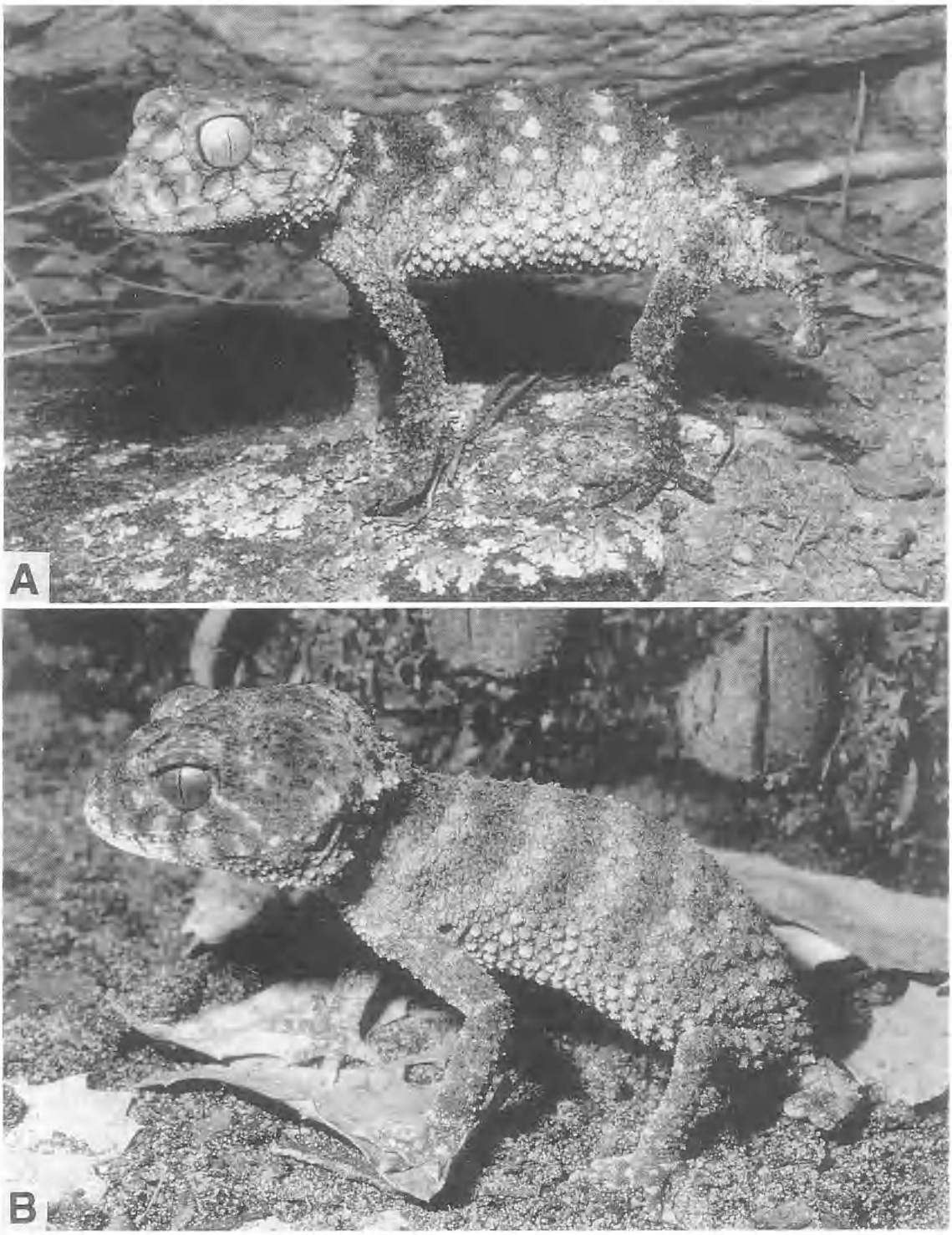

FIG. 2. *Nephrurus asper*. A, Moura, QLD; B, Broad-banded form, Heathlands, Cape York Peninsula, QLD. (Photographs: S. Wilson).

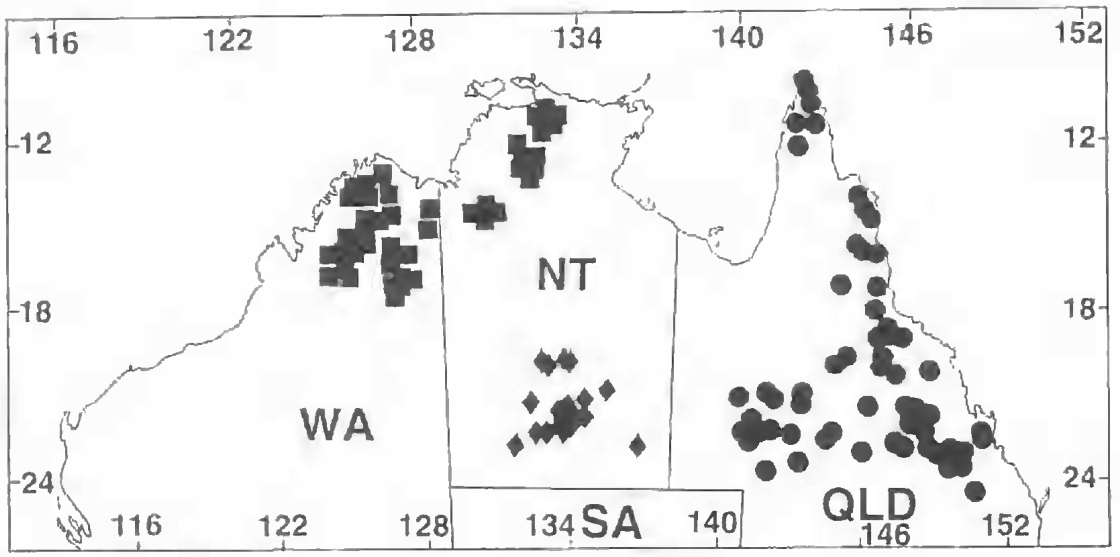

FIG. 3. Distribution of the *Nephrurus asper* species complex. *N. amyae* (diamonds), *N. asper* (circles), *N. sheai* (squares).

contained legs from a medium-sized grasshopper (Acrididae), fragments of a large scorpion (*Urodacus* sp.) and fragments of a small phasmid.

REMARKS

A clear photograph of the holotype of *N. asper* (BMNH1946.8.23.34) was provided by Bauer, (1990). The narrow, irregular dorsal crossbands and moderate, uniform rump scalation of this specimen are consistent with the pattern and scalation of QMJ56088, a specimen reeently collected only 14km from the type locality. Further, these speeimens are morphologically/phenotypically consistent with populations of spinose *Nephrurus* occurring in Queensland between 18°19'S & 25°21'S. These are regarded here as *N. asper*. The broad-banded form on CYP is also included in *N. asper* because it cannot be signifieantly separated from this speeies by scalation features or body proportions, and preliminary genetic data show a low level of divergence between a specimen from Heathlands, CYP and a specimen from the Capella region of MEQ (Couper & Donnellan, unpubl. data)

The broad-banded CYP colour form is narrowly separated from the narrow-banded form at the southern limit of its range. Tim Hawkes (Cape York Herpetological Society) has provided colour transpareneies of a broad-banded specimen from 6km east of Almaden (17°21'S, 144°43'E) and a narrow-banded specimen from approximately 87km south, near the junetion of the Kennedy and Gulf Redevelopmental Highways (18°09', 144°41'). This narrow-banded specimen is approximately 75km NE of the most southerly museum record of the broad-banded form (QMJ57993). Clearly, the range of both colour forms overlap latitudinally but, to date, they have not been found in sympatry.

Nephrurus amyae Couper sp. nov.
(Fig. 4; Statistieal analyses group 3)

Nephrurus asper; Cogger, 1992 (in part).

MATERIAL EXAMINED

HOLOTYPE: AMR104458, Winnecke Goldfields, Garden Stn, N of Alice Springs, NT (23°17'S 134°25'E). Found in mine tunnel, February, 1982. Don. M. Robinson.

PARATYPES: NORTHERN TERRITORY: QMJ51650, 15km SE of Glen Helen (23°31'S 132°21'E); QMJ53650, Hugh R, nr Alice Springs (23°49'S 133°22'E); AMR49716, Mt Gillen, Alice Springs (23°42'S 133°48'E); AMR50542, Alice Springs (23°42'S 133°53'E); AMR11965, Mt Gillen, Alice Springs (23°43'S 133°48'E); AMR90198, Jay Ck, NT (23°50'S 133°29'E); AMR10371, between Hale and Plenty Rivers, Central Australia (24°25'S 136°10'E); NMVD538, Barrow Ck, (21°32'S 133°53'E); NMVD51919-21, 28.9km S of Barrow Ck (21°45'S 133°40'E); NMVD55377, nr Alice Springs (23°42'S 133°52'E); NMVD12684-5, Central Australia; SAMR1892, Barrow Ck (21°32'S 133°53'E); SAMR38837, Mt Zeil (23°25'S 132°25'E); SAMR40561, approx 35km SE of Kings Ck Homestead (24°26'S 131°49'E); SAMR30523, No Locality data; NTMR441, Barrow Ck (21°32'S 133°53'E);

R14096, Mt Riddock Stn, Dulcie Ra. (22°30'S 135°25'E); NTMR33717, Winnecke Goldfields (23°02'S 134°23'E); NTMR33716, Bond Springs Stn (23°34'S 133°52'E); NTMR12377, 16km N Alice Springs (23°34'S 133°53'E); NTMR33720, Alice Springs Hills, 19 Mile Bore (23°35'S 133°52'E); NTMR33722-3, Alice Springs, Wigleys Turnoff (23°36'S 133°53'E); NTMR12380, 9km N Alice Springs (23°37'S 133°53'E); NTMR33721, Alice Springs, Charles R (23°39'S 133°51'E); NTMR5586, NTMR5969, NTMR14991, Alice Springs (23°42'S 133°52'E); NTMR33724, NTMR33726, Alice Springs (23°42'S 133°53'E); NTMR5383, Alice Springs Power House (23°42'S 133°55'E); NTMR5466, Alice Springs, Mt Gillen (23°43'S 133°48'E); NTMR2458, Alice Springs, Emily Gap (23°45'S 133°57'E); NTMR33719, Hermannsburg, Finke Crossing (23°58'S 132°46'E); NTMR33715, Krichauff Ra. (23°59'S 132°38'E); NTMR33728, No data.

DIAGNOSIS

N. amyae is the largest and most spinose member of the *N. asper* species group. Its large size distinguishes it from other members of this group (max SVL 135mm vs 114mm *N. asper*, 121mm *N. sheai*). It is further distinguished from *N. asper* and *N. sheai* by the spinosity of the its rump and thighs (extremely spinose vs moderately spinose). The arrangement of the basal scales surrounding the tubercules on the rump and thighs also separates *N. amyae* from *N. asper* and *N. sheai*. In *N. amyae* the basal scales are irregular in size and in most specimens examined, some of the basal scales are greater than half the height of the central scale. In *N. asper* and *N. sheai* the basal scales are uniform in size and less than half the height of the central scale.

In the KS2 analysis *N. amyae* and *N. asper* (excluding broad-banded CYP specimens which are not significantly separable from other QLD populations of this species) show significant separation of the shape of frequency distributions for; KW, HW, S, NL, R & I. *N. amyae* and *N. sheai* show significant separation of the shape of frequency distributions for; KW, HW, HL, S, NL, SL, IL, R & I (Table 1).

DESCRIPTION

SVL(mm): 50-135 (N 40, mean 100.3). Proportions, (%SVL): - L1 - 38.1-52.4 (N 40, mean 42.7), L2 - 42.5-56.1 (N 40, mean 48.4), AG - 35.4-53.5 (N 40, mean 45.1), T - 12.3-17.5 (N 37, mean 15.0), TV - 15.2-25.2 (N 37, mean 21.3), HL - 27.7-34.2 (N 38, mean 30.4), HW - 23.9-30.6 (N 38, mean 26.4), HD - 10.5-15.1 (N 38, mean 13.2), S - 9.1-12.9 (N 39, mean 10.5), EE - 10.2-14.8 (N 39, mean 12.9), NL - 10.4-19.9 (N 37, mean 14.7).

Head. Large and deep, covered with small, round to hexagonal, juxtaposed scales. Posteriorly bearing scattered tubercules intermixed with the smaller scales. Each tubercule consists of a high central scale, circled by a ring of smaller basal scales. Tubercules most prominent on the nape. Dorsal skin co-ossified with skull. Nostril small, opening upwards and backwards. Eye large with vertical pupil. Ear vertically elongate, tympanum deeply recessed. Rostral scale small, with 7-18 (N 39, mean 9.7) scales in direct contact with dorsal edge. Interorbital scales 6-11 (N 40, mean 8.0). Supralabial scales 11-17 (N 78, mean 13.5). Infralabial scales 11-17 (N 78, mean 13.4).

Neck. Broad, less than half width of head.

Body. Stout, dorsal and ventral surfaces with small granular scalation. Granular scales intermixed with larger conical tubercules on dorsal and lateral surfaces. Mid-dorsal tubercules small, rump tubercules large (extremely pronounced) except in juveniles. Basal scales surrounding rump tubercules irregular. In many specimens, some are greater than half the height of the central scale. Rump tubercules larger than flank tubercules. Rump tubercules larger than nape tubercules (90% material examined) or subequal to nape tubercules (10% material examined). Lower flanks and ventral surface with scattered, slightly raised rosettes which vary between being pronounced or barely discernible.

Limbs. Long and slender, bearing enlarged tubercules on dorsal surfaces. Tubercules on thighs largest (extremely pronounced). Basal scales surrounding thigh tubercules irregular. In many specimens some are greater half the height of the central scale. Digits short, cylindrical, undilated distally and terminating in a non-retractile claw. Third toe on hindlimb longest.

Tail. Short, moderately depressed, constricted at base and terminating in a globular, kidney-shaped knob (KW 21.3-35.0 %T, N 36, mean 27.6). Four longitudinal rows of tubercules present on dorsal and lateral surfaces. Basal scales surrounding caudal tubercules less than half the height of the central scale. Caudal annuli 8-13 (N 37, mean 10.4).

The measurements and scale counts for the holotype (AMR104458) are as follows; SVL 135.0mm, L1 54.1mm, L2 63.1mm, T 19.4mm, TV 23.3mm, HL 40.0mm, HW 34.4mm, HD 17.4mm, S 12.8mm, EE 18.4mm, NL 14.9mm, KW 4.5mm, R 8, I 7, SL 15/15, IL 14/14, TA 10.

FIG. 4. *Nephrurus amyae*. Kings Ck Stn, southwestern NT. (Photograph: S. Wilson).

This species has been illustrated previously as *N. asper* (e.g. Hoser, 1989: 74).

PATTERN

Body. In spirit, fawn to mid brown on dorsal surface. Many specimens with a black band present on the nape. Some specimens with seven to nine obscure, broken crossbands. These appear as a series of spots with each spot covering a tubercule. Others with no indication of banding or with obscure blotches along the vertebral line. Fine black lines form a reticulated pattern on the dorsum and upper lateral zone. These lines fade in larger specimens. Ventral surface cream.

Limbs. Lacking irregular crossbands distally. Digits unbanded but sometimes obscurely mottled.

Tail. As for body, with an obscure, broad, pale crossband on proximal half.

Head. Often paler than body. Covered on top and sides with fine black reticulations which form an intricate pattern. These fade in larger specimens.

ETYMOLOGY

For Amy Couper.

DISTRIBUTION

Confined to the hill country of the south-central NT centred around Alice Springs (23°42'S, 133°53'E), extending north to Barrow Ck (21°32'S, 133°53'E) (Fig. 3).

HABITAT

N. amyae favours open ground on rocky substrates in open woodland habitats. It may be found associated with a scattered *Triodia* groundcover.

REPRODUCTIVE NOTES

Clutch size two eggs. Females (NTMR33722-23, NTMR5466) had small vitellogenic follicles on their ovaries between mid October - late December (<5.5mm diameter). NTMR2458, collected in mid March, had a greatly enlarged follicle in each ovary (the largest of these follicles measured 14.58mm × 13.0mm). Bedford and Christian (1993) provide clutch data for a specimen from Gardens Station, 75km northeast of Alice Springs. Two eggs measuring 34.3mm × 16.6mm and 37.0mm × 16.1mm were laid on the 17/18 February 1992. These weighed 5.6g

and 5.8g respectively. The total clutch was 24.8% of the non-gravid female mass.

Three males (NTMR33719, NTMR33721 & NTMR441) collected between early October - late November appeared to be in reproductive condition (epididymis enlarged and turgid).

DIETARY NOTES

The gut of NTMR33723 contained a large centipede (Chilopoda: Scolopendridae), as did QMJ51650. QMJ53650 contained an ant head (Hymenoptera: Formicidae), the hind legs of a grasshopper (Orthoptera: Acrididae) and many medium-sized cockroach fragments (Blattodea: Blattidae).

REMARKS

N. amyae is one of Australia's largest geckos in terms of SVL and weight (max SVL 135mm, AMR104458). It is exceeded in length only by *Saltuarius cornutus* (max SVL 145mm) and *S. salebrosus* (max SVL 141mm). However, despite its greatly reduced tail size, it is substantially heavier than both of these species and weighs a maximum of 65g (AMR104458). AMR104458 was compared in weight to a number of other large Australian gecko species held in the AM and QM collections. The results are as follows: *Carphodactylus leavis* QMJ54312 (SVL 107mm, weight 26g); *Cyrtodactylus louisiadensis* QMJ38198 (SVL 130mm, weight 46g); *Rhacodactylus australis* QMJ39723 (SVL 110mm, weight 27g); *Saltuarius cornutus* QMJ48179 (SVL 140mm, weight 49g), QMJ30991 (SVL 137mm, weight 57g), AMR42163 (SVL 145mm, weight 43g); *S. salebrosus* QMJ22288 (SVL 141mm, weight 57g) and *S. swaini* QMJ51640 (SVL 131mm, weight 43g).

Nephrurus sheai Couper sp. nov.
(Fig. 5; Statistical analyses group 1)

Nephrurus asper; Cogger, 1992 (in part).

MATERIAL EXAMINED

HOLOTYPE: NTMR11470, Bowerbird Camp, Magela Ck, NT (12°47'S 133°07'E), coll. I. Archibald and J. Bywater, 01 September, 1983.

PARATYPES: QMJ52872, March Fly Glen, Gibb R Rd, Kimberley, WA; QMJ57515, 10km SE of Oenpelli, NT (12°22'S 133°07'E); AMR93181, Jabiluka Project area, NT (12°29'S 132°54'E); AMR93182, Jabiluka Project area, NT (12°31'S 132°57'E); AMR88668, Jabiluka Project area, NT (12°34'S 132°55'E); AMR13403, Katherine, NT (14°28'S 132°16'E); AMR12876, Manbullo Stn, NT (14°31'S 132°12'E); AMR72980, Jasper Gorge, NT (16°02'S 130°40'E); AMR140279, Manning Gorge, Mt Barnett Stn, WA (16°39'31"S 125°55'37"E); NMVD4552, Pine Ck, NT (13°49'S 131°50'E); SAMR3597, Moolabulla, WA (18°12'S 127°30'E); WAMR13646, WAMR27374 Kalumburu, WA (14°18'S 126°38'E); WAMR47587, 8km N of Katherine, NT (14°25'S 132°12'E); WAMR43153, WAMR77269, WAMR77581, WAMR77585 Mitchell Plateau, WA (14°49'S 125°50'E); WAMR56423, King Edward R Crossing, WA (14°52'S 126°12'E); WAMR50460, Drysdale R NP, WA (15°09'S 127°06'E); WAMR46782, Prince Regent R, WA (15°19'S 125°35'E); WAMR73903, Ellenbrae Stn, WA (15°57'S 127°04'E); WAMR60343, WAMR60947, Jasper Gorge 53km NW of Victoria River Downs Homestead, NT (16°02'S 130°41'E); WAMR60362, Jasper Gorge 53km NW of Victoria River Downs, NT (16°02'S 130°45'E); WAMR57123-7, Gibb R Crossing 47km N of Gibb River Stn, WA (16°06'S 126°31'E); WAMR52661, WAMR86927, Lake Argyle (Ord R), WA (16°07'S 128°44'E); WAMR83359, 24km NW of Mt Elizabeth Homestead, WA (16°11'S 126°00'E); WAMR70562, 3.5km at 288° from (new) Lissadell Homestead, WA (16°39'S 128°31'E); WAMR73904, Mt Barnett Stn, WA (16°40'S 125°57'E); WAMR56466, Plain Ck, Beverley Springs Stn, WA (16°43'S 125°23'E); WAMR83531-2, Galvans Gorge, WA (16°48'S 125°51'E); WAMR64731, 4.5km at 140° from Clancys Yard, WA (17°07'S 125°35'E); WAMR70551, 9.5km at 256° from Inglis Gap, WA (17°07'S, 125°05'E); WAMR57118, Inglis Gap, King Leopold Range, WA (17°08'S 125°10'E); WAMR70552, 8.6km at 167° from Mt Amy (Napier Downs Stn), WA (17°14'S 124°54'E); WAMR58671, 20km ENE of Tableland, WA (17°14'S 127°01'E); WAMR58636, 25km SE of Bedford Downs Homestead, WA (17°27'S 127°36'E); WAMR58647, 10km SE of Lansdowne Homestead, WA (17°41'S, 126°48'E); WAMR1340, Leopold Downs, WA (17°52'S 125°25'E); WAMR12614, Calwynyardah, WA (18°00'S 124°47'E); WAMR70029, 43km at 316° from Fitzroy Crossing P.O., WA (18°00'S 125°30'E); WAMR48175, Moola Bulla, WA (18°11'S 127°30'E); WAMR26633, Halls Ck, WA (18°13'S 127°39'E); WAMR87092, 8km SW of Halls Ck, WA (18°16'S 127°37'E); WAMR46116, Margaret River Homestead, WA (18°38'S 126°57'E); WAMR87082, 0.5km N of Mary Pool, WA (18°43'S 126°53'E); NTMR12605, Nabarlek, NT (12°19'S 133°19'E); NTMR17822, 10km SE Oenpelli, NT (12°22'S 133°07'E); NTMR12493, Magela Ck, Bowerbird Camp, NT (12°47'S 133°05'E); NTMR11464, Magela Ck, Bowerbird Camp, NT (12°47'S 133°07'E); NTMR4027, NTMR4272, Jim Jim Falls, NT (13°17'S 132°50'E); NTMR387, Katherine, 4.7mi N, NT (14°27'S 132°15'E); NTMR3759-61, Katherine, 4km N, NT (14°27'S 132°15'E); NTMR267, NTMR297, Katherine, NT (14°28'S 132°16'E); NTMR2377, Katherine, Lower Farm Rd, NT (14°35'S 132°12'E); NTMR33718,

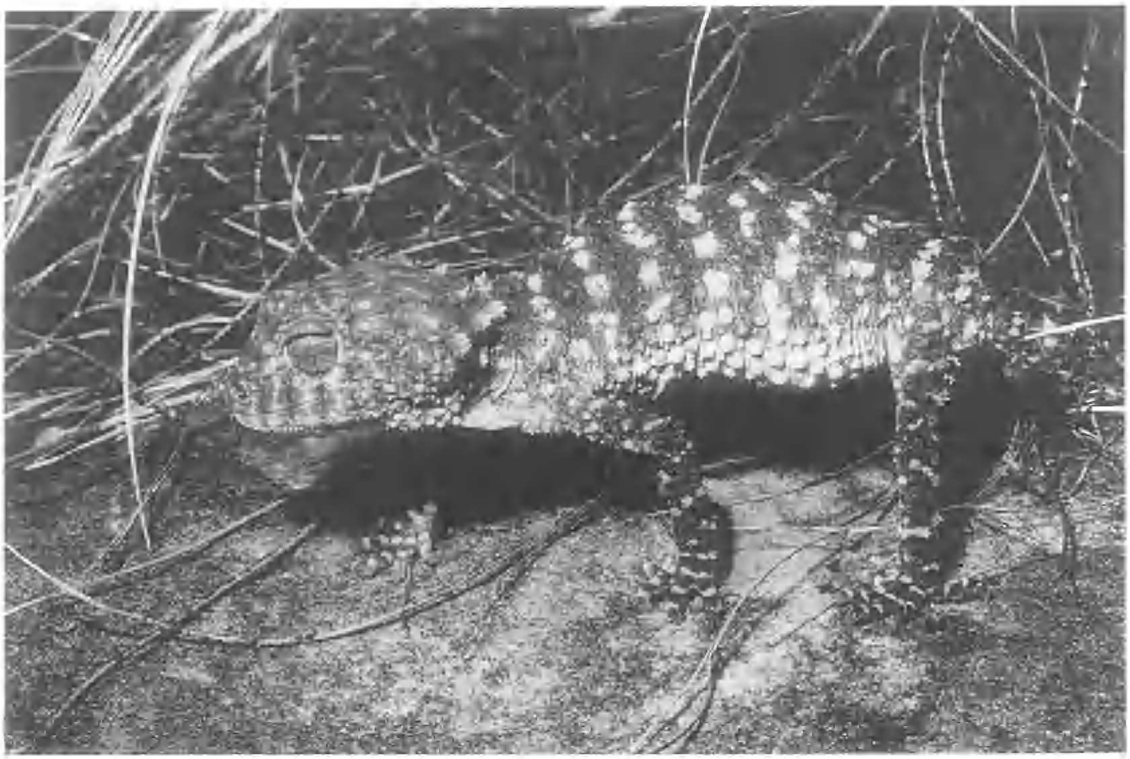

FIG. 5. *Nephrurus sheai*. Manning Gorge, Gibb R Track, Kimberley region, WA. (Photograph: G. Harold).

Wickham R, Victoria River Downs, NT (16°05'S 130°35'E); NTMR13485, Gregory NP, Bullita area, NT (16°07'S 130°26'E).

DIAGNOSIS

N. sheai is a large, moderately spinose member of the *N. asper* species group. *N. sheai* is distinguished from *N. asper* and *N. amyae* by the colour pattern of its digits (digits strongly marked with alternating bands of brown and white vs digits not strongly banded with brown and white); also by size (max SVL 121mm vs 114mm *N. asper*, 135mm *N. amyae*). It is further distinguished from *N. amyae* by the spinosity of the its rump and thighs (moderately spinose vs extremely spinose). The arrangement of the basal scales surrounding the tubercules on the rump and thighs also separate *N. sheai* and *N. amyae*. In *N. sheai* the basal scales are uniform in size and less than half the height of the central scale. In *N. amyae* the basal scales are irregular in size and in most specimens examined, some of the basal scales are greater than half the height of the central scale.

In the KS2 analysis *N. sheai* and *N. amyae* show significant separation of the shape of frequency distributions for; KW, HW, HL, S, NL, SL, IL, R & I. *N. sheai* and *N. asper* (excluding broad-banded CYP specimens which are not significantly separable from other QLD populations of this species) show significant separation of the shape of frequency distributions for; T, TV, KW, TA, NL, SL, IL, & I. (Table 1).

DESCRIPTION

SVL(mm): 42.3-121.4 (N 69, mean 82.8). Proportions,(%SVL): - L1 - 37.9-50.7 (N 69, mean 44.0), L2 - 45.0-59.1 (N 69, mean 49.8), AG - 35.2-52.4 (N 67, mean 43.9), T - 10.1-21.7 (N 68, mean 14.8), TV - 14.1-26.4 (N 68, mean 19.8), HL - 28.4-34.3 (N 68, mean 31.2), HW - 23.6-31.7 (N 69, mean 27.5), HD - 11.0-16.1 (N 69, mean 13.6), S - 9.4-13.0 (N 69, mean 11.0), EE - 10.9-15.1 (N 69, mean 12.8), NL - 8.6-18.0 (N 68, mean 14.6).

Head. Large and deep, covered with small, round to hexagonal, juxtaposed scales. Posteriorly bearing scattered tubercules intermixed with the smaller scales. Each tubercule consists of a high central scale, circled by a ring of smaller basal scales. Tubercules most prominent on the nape. Dorsal skin co-ossified with skull. Nostril small, opening upwards and backwards. Eye

large with vertical pupil. Ear vertically elongate, tympanum deeply recessed. Rostral scale small, with 7-18 (N 69, mean 12.4) scales in direct contact with dorsal edge. Interorbital scales 8-15 (N 66, mean 10.5). Supralabial scales 12-20 (N 138, mean 15.8). Infralabial scales 11-20 (N 137, mean 16.1).

Neck. Broad, less than half width of head.

Body.Stout, dorsal and ventral surfaces with small granular scalation. Granular scales intermixed with larger conical tubercules on dorsal and lateral surfaces. Mid-dorsal tubercules small, rump tubercules small to large. Basal scales surrounding rump tubercules uniform, less than half as high as the central scale. Rump tubercules larger than flank tubercules (85% material examined) or subequal to flank tubercules (15% material examined. Rump tubercules smaller than nape tubercules (41% material examined) or subequal to nape tubercules (59% material examined). Lower flanks and ventral surface with scattered, slightly raised rosettes which vary between being pronounced or barely discernible.

Limbs. Long and slender, bearing enlarged tubercules on dorsal surfaces. Tubercules on thighs largest, with uniform basal scales less than half as high as the central scale. Digits short, cylindrical, undilated distally and terminating in a non-retractile claw. Third toe on hindlimb longest.

Tail. Short, moderately depressed, constricted at base and terminating in a globular, kidney-shaped knob (KW 21.2-47.9 %T, N 67, mean 31.5). Four longitudinal rows of tubercules present on dorsal and lateral surfaces. Basal scales surrounding caudal tubercules uniform and less than half as high as the central scale. Caudal annuli 8-12 (N69, mean 9.7).

The measurements and scale counts for the holotype (NTMR11470) are as follows; SVL 106.8mm, L1 45.3mm, L2 52.5mm, T 15.5mm, TV 21.4mm, HL 32.5mm, HW 29.8mm, HD 13.3mm, S 10.9mm, EE 14.3mm, NL 17.4mm, KW 4.6mm, R 13, I 11, SL 18/17, IL 16/15, TA 11.

This species has been illustrated previously as *N. asper* (e.g. Storr et. al., 1990: 82, pl.1; Schmida, 1985: 103).

PATTERN

Body. In spirit, tan - greyish brown on dorsal surface. Many specimens have a broad black band on the nape. Seven - 11 narrow, irregular, cream crossbands present between head and hindlimbs. Crossbands range from obscure to bold and are continuous or broken into a series of spots, with each spot covering a tubercule. In most specimens fine black lines lie between the cream crossbands. These black lines are sometimes interconnected to form a reticulated pattern. Ventral surface cream, sometimes faintly marbled with grey or brown.

Limbs. Often with irregular crossbands on the distal half. Digits heavily banded with brown and white.

Tail. As for body, with an obscure, broad, pale crossband on proximal half.

Head. Tan, usually paler than the body. Covered dorsally and laterally with fine black reticulations which form an intricate pattern. These lines are most prominent in juveniles and may fade in larger specimens.

ETYMOLOGY

For Glenn Shea.

DISTRIBUTION

Confined to hill country from the Kimberley Region of WA to the Arnhem Escarpment in the NT (Fig. 3).

HABITAT

N. sheai favours rocky substrates in open woodland habitats. It is frequently associated with a scattered *Triodia* ground-cover (G. Harold, pers. comm.). The holotype (NTMR11470) was collected from a rocky outcrop in mid-high open forest with a grass understorey.

REPRODUCTIVE NOTES

Clutch size - usually two eggs, although a single egg clutch has been recorded (How et. al., 1990). Gravid females are present in the population in January - WAMR86927, WAMR27374; February- WAMR87092 and June - NTMR33718. WAMR70551 had a greatly enlarged vitellogenic follicle (12.42 × 10.83mm) in the ovary in May. Incubation of the eggs takes 115 days at a mean temperature of approximately 25°C (Ehmann, 1992). Gow, 1979 recorded the measurements of two eggs laid on 5 Dec 1973 (30 × 16.5mm and 29 × 15.5mm). Males were in reproductive condition (epididymis enlarged and turgid) in November - WAMR56423, NTMR267 and in February - WAMR48175. How et al. (1990), record reproductive activity extending over at least nine months (spanning the October-April wet period) for *N. sheai* in WA and suggest that reproductive activity may occur throughout the year.

DIETARY NOTES

The gut of QMJ57515 contained moth or caterpillar cuticle with dense, short hairs. QMJ52872 contained numerous termite heads (*Nasutitermes* sp.).

REMARKS

AMR125387 was collected from Cadell Ck, near Hamilton, western QLD. This specimen has strongly banded toes, a diagnostic feature of *N. sheai*. Its occurrence in Queensland is not consistent with the overall distribution pattern of this species. Further, of the QLD material examined in this study (79 × *N. asper*), AMR125387 is the only specimen to possess strongly banded toes. Because of these inconsistencies, this specimen has not been included in the material examined for either *N. sheai* or *N. asper*. The status of this specimen is uncertain. We believe there has been an error with the collection data.

KEY TO *N. ASPER* SPECIES COMPLEX

1. Digits strongly banded brown and white . . . . . *N. sheai*
   Digits not strongly banded 2
2. Tubercules of the rump and thighs extremely pronounced, usually much larger than those covering the rest of the dorsum . . . . . *N. amyae*
   Tubercules of the rump and thighs small to moderate . . . . . *N. asper*

ACKNOWLEDGEMENTS

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LITERATURE CITED

ANON. 1952-69. 'Atlas of Australian resources'. (Department of National Development: Canberra).

BAUER, A. M. 1990. Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia:Gekkonidae). Bonner Zoologische Monographien 30: 1-217.

BEDFORD, G. & CHRISTIAN, K. 1993. Egg size of the Prickly Knob-tailed Gecko (*Nephrurus asper* Gunther, 1876) with a preliminary comparison of investment per progeny among geckos. Dactylus 1(4):38-41.

CAMERON, E.E. & COGGER, H. G. 1992. The herpetofauna of the Weipa region, Cape York Peninsula. Technical Reports of the Australian Museum 7: 1-200.

COGGER, H. G. 1992. 'Reptiles and amphibians of Australia', 5th ed. (Reed: Sydney).

COGGER, H. G., CAMERON, E.E. & COGGER, H. M. 1983. Amphibia and Reptilia. Pp1-200. In Walton, D.W. (exec. ed.), 'Zoological catalogue of Australia, Vol. 1'. (Australian Government Publishing Service: Canberra).

COUPER, P. J., COVACEVICH, J. A. & MORITZ, C. 1993. A review of the leaf-tailed geckos endemic to eastern Australia: a new genus, four new species, and other new data. Memoirs of the Queensland Museum 34(1): 95-124.

EHMANN, H. 1992. 'Encyclopedia of Australian animals: reptiles'. (Angus & Robertson: New South Wales).

GOW, G. 1979. Notes on the biology of *Nephrurus asper*. Northern Territory Naturalist 1(2): 19-20.

GÜNTHER, A. 1876. Descriptions of new species of reptiles from Australia collected by Hr. Dämel for the Godeffroy Museum. Journal Des Museum Godeffroy. Geographische, ethnographische und naturwissenschaftliche Mitteilungen 5: 45-47.

HOSER, R.T. 1989. 'Australian reptiles & frogs.' (Pierson & Co: Sydney).

HOW, R. A. DELL, J. & WELLINGTON, B.D., 1990. Reproductive and dietary biology of *Nephrurus* and *Underwoodisaurus* (Gekkonidae) in Western Australia. Records of the Western Australian Museum 14(4): 449-459.

KOLMOGOROV, A. 1941. Confidence limits for an unknown distribution. Annals of Mathematical Statistics 12: 461-463.

RAO, C.R. 1952. 'Advanced statistical methods in biometric research.' (New York: Wiley).

SCHMIDA, G. 1985. 'The cold-blooded Australians.' (Doubleday Australia Pty Ltd: Sydney).

SMIRNOV, N.V. 1939. On the estimation of the discrepancy between empirical curves of distribution

for two independent samples. Bulletin of Mathematics, University of Moscow 2: 1-16.

STORR, G.M. 1963. The gekkonid genus *Nephrurus* in Western Australia, including a new species and three new sub-species. Journal of the Royal Society of Western Australia 46: 85-90.

1988. Three new *Diplodactylus* (Lacertilia: Gekkonidae) from the arid zone of Australia. Records of the Western Australian Museum 14(2): 217-223.

1989. A new *Heteronotia* (Lacertilia: Gekkonidae) from Western Australia. Records of the Western Australian Museum 14(3): 269-273.

STORR, G.M., SMITH, L.A. & JOHNSTONE, R.E. 1990. 'Lizards of Western Australia, Vol. 3, geckos & pygopods.' (Western Australian Museum: Perth).

WALSH, J.E. 1965. 'Handbook of nonparametric statistics', Vol. 2. (Princeton: Van Nostrand).

WILSON, S. K. & KNOWLES, D. G. 1988. 'Australia's reptiles'. (Collins Australia: Sydney).